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## REPRINT

RECORDS OF BIOGEOGRAPHY IN THE OCEAN

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## Records of Bioluminescence in the Ocean<sup>1</sup>

BRIAN P. BODEN and ELIZABETH M. KAMPA<sup>2</sup>

DURING THE MONTH of June, 1955, while measurements were being made of the depth of penetration of moonlight into the sea off the Kona Coast (S. W. coast) of the island of Oahu in the Hawaiian group, some information was obtained on bioluminescence in deep water in this region and on the effect of moonlight on the vertical distribution of luminescent organisms. Observations of bioluminescence were also made off San Diego, California, during the month of January, 1956.

An underwater photometer (Kampa, 1955; Snodgrass *et al.*, 1957 in press) designed for work in the deep sonic-scattering layers was used for these measurements. This was equipped with a depth-indicator (Boden *et al.*, 1955) so that a precise knowledge of the depth of the instrument was available at all times. The instrument utilizes a 931-A photomultiplier tube oriented with the sensitive surface facing up. In front of this is a collimating tube at the base of which is a filter-holder for interference filters. The collimator ensures that the 5° useful angle of the filters

is not exceeded. At the distal end of this tube is a diffusing plastic disc, which is a true Lambert-type collector—that is, under a uniform sky the intensity ( $I_\theta$ ) collected from the direction  $\theta$  would be

$$I_\theta = I_0 \cos \theta.$$

Thus the instrument measures irradiance. The collimating tube and filter-holder are free-flooding. The dark-current level of the instrument changes less than 0.2 millivolts on the 0–10 millivolt recorder range through the temperature range 10–30°C. It fluctuates about 0.03 millivolts at any particular temperature. The instrument registers down to  $1 \times 10^{-6} \mu$  watts  $\text{cm}^2$ .

Observations of bioluminescence in surface waters were made off San Diego (Lat. 32° 38' N., Long. 117° 35' W.) on the morning of January 18, 1956.

The photometer was lowered with its sensitive surface pointed downward. The sky was cloudless and moonless, and the first cast was made immediately before the beginning of official twilight. Luminescence was clearly visible at the surface at this time, and porpoises were seen to leave bright trails of light in their wakes.

Flashes, or bursts of light, were observed by the instrument, and recorded on a Leeds and Northrup Speedomax recorder from the surface to a depth of 60 meters. From a depth of about 25 meters downward the flashes were superimposed on the dark-current level of

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<sup>2</sup> Scripps Institution of Oceanography, University of California, La Jolla, California. Manuscript received February 27, 1956.



the instrument, and at times apparently single flashes reached a level of  $2 \times 10^{-3} \mu$  watts/cm<sup>2</sup>.

A later cast, with the photometer still pointed downward, revealed that at sunrise (0652 hrs.) the flashes were first recorded at a depth of about 110 meters.<sup>3</sup> All facts known to us indicate that these flashes are generated *in situ* and we interpret them as due to luminescent organisms, possibly both nekton and plankton.

Records of bioluminescence at depth were first made in Hawaii at midnight on the night of June 9, 1955. The moon, three days past the full, had just appeared over the mountains. Its angle of elevation at 2400 hours was 19°. The instrument was lowered without color filters, and total irradiance, as seen by the instrument, was recorded. The sky was partly cloudy, but the moon remained clear throughout the observations.

Figure 1 is a tracing of the actual recording made on the Leeds and Northrup Speedomax recorder. Total irradiance ( $H$ ) at any depth was obtained from

$$n = k H = \int_0^{\infty} E S d\lambda,$$

where  $n$  = recorder reading,  $E$  = energy of the source through the wave-length interval  $d\lambda$ ,  $S$  = relative spectral sensitivity of the

<sup>3</sup> The possibility that these are artifacts due to instrument failure is to be considered. It is improbable that distortion due to pressure affected the circuitry, for the phenomenon was not observed when the instrument had been lowered to greater depths during daylight. It is improbable, too, that the effect could have been caused by water leakage, for moisture in the system has been shown to raise the dark current to such a high level that the recorder is immediately sent off scale. Furthermore the fact that color filters placed in the light-path reduced the amplitude of recorded flashes discounts the possibility that loose electrical connections were responsible. Another photometer, similar to the one employed here, has since shown that the flashes are not recorded when the sensitive element is covered but are when it is exposed immediately afterward at the same depth. Thus we believe that the instrument was sensing real light flashes.

Flashes of this nature could not have been caused by tilt of the instrument since it was pointed downward.

Photomultiplier tube through the wave-length interval,  $d\lambda$  (300–700 m $\mu$ ). The value of  $k$  was obtained by calibration of the entire instrument against a Bureau of Standards source. The inset shows the relative spectral sensitivity of the 931-A tube used.

The dark-current level of the photometer was reached at 200 meters. From about 50 meters downward numerous brilliant flashes of light were recorded.

At some depths, for example 120–130 meters and 150–170 meters, the background light level appears to have remained constant or to have increased rather than to have decreased with depth.

Many types of luminescent marine animals, e.g., euphausiids, generate a steady glow of light for limited periods in contrast with the discrete flashes produced by others (Harvey, 1940). Possibly the sustained light level (Fig. 1) on which the flashes are superimposed at depths of 120–130 meters and 150–170 meters was due to a background glow produced by concentrations of such types, or by numerous flashes at varying distances.

An alternative explanation of the flashes can be found by visualizing a distribution of steadily-glowing organisms similar to that of stars in the sky, and a flashlike increase in the level of light due simply to the instrument's approach to and retreat from a glow during its descent. The rate of descent of the instrument was about 32 meters/minute. For this to be the true explanation, the glows would have had to be about 1 meter of depth apart, for the frequency of the flashes was about 36/minute.

Many luminescent organisms flash brightly when irritated mechanically or chemically. It is impossible at present to determine whether the observed flashes were due to spontaneous luminescence or whether the luminescence was intensified by agitation of the animals by the instrument.

Four more casts were made, using narrow-band interference filters, during the forty-five minutes after midnight. The angle of eleva-

tion of the moon varied between  $21^\circ$  and  $31^\circ$  during this period. The interference filters employed were G. A. B. filters, manufactured in Liechtenstein, with half-peak band widths

of about  $10\text{ m}\mu$ . Block filters are incorporated to reduce stray light and eliminate secondary transmission peaks. Peak transmissions, measured by a Beckman Model DU spectrophotom-

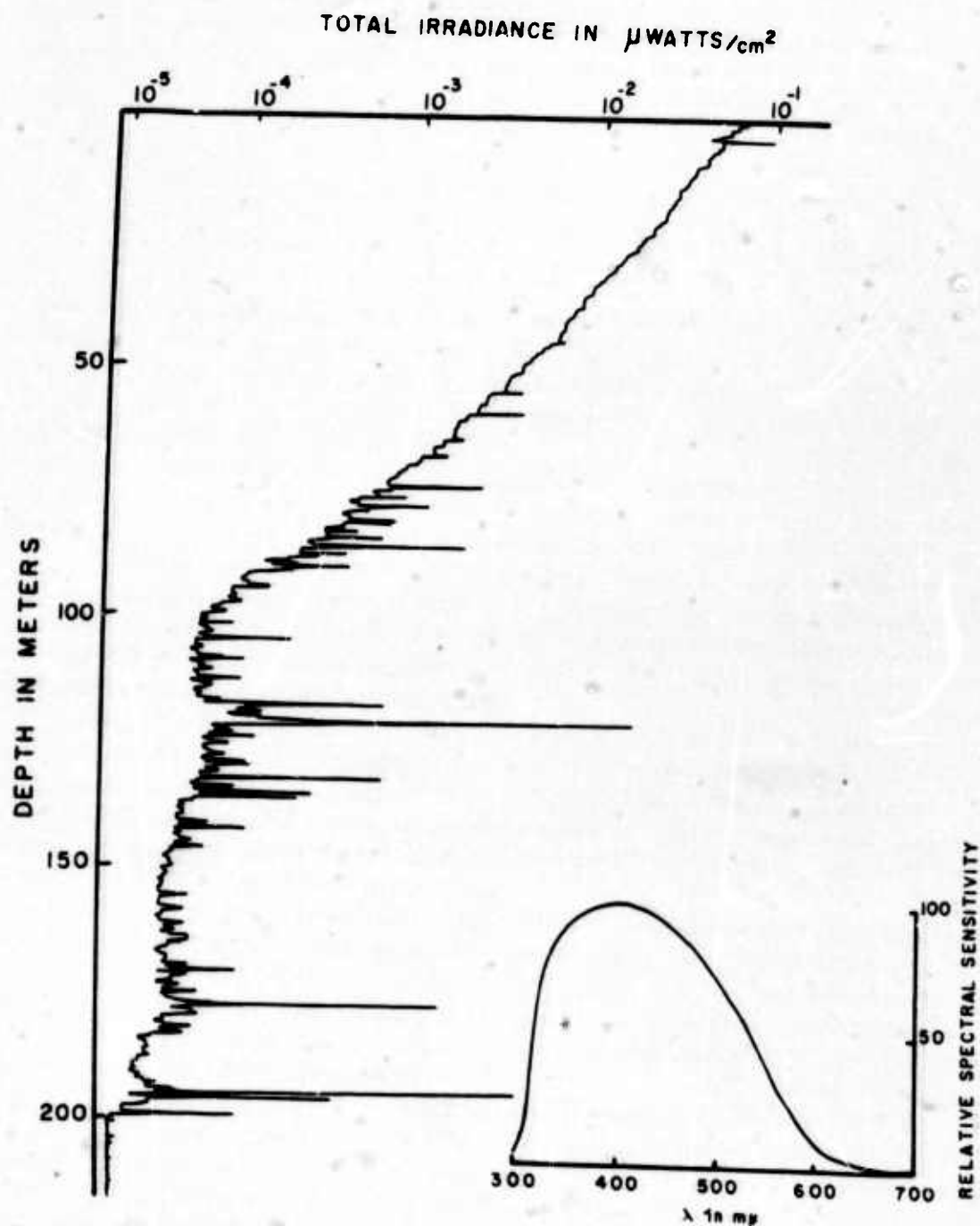


FIG. 1. Tracing of total irradiance recorded on Leeds and Northrup Speedomax recorder by bathyphotometer without color filters. Spectral sensitivity of the 931-A photomultiplier tube is shown in inset. This is from manufacturer's specifications and is an average curve. The record was made at 2400 hours, June 9, southwest of Oahu.

erer, are at 418, 491, 552, and 630  $m\mu$  (see inserts in Fig. 2).

Irradiance ( $H$ ) was obtained from

$$n = k H = \int E T_f S d\lambda,$$

where  $n$  = recorder reading,  $E$  = energy of the source through the wave-length interval  $d\lambda$ ,  $T_f$  = measured transmission of the individual interference filter through the wave-length interval  $d\lambda$ , and  $S$  = the relative sensitivity of the photomultiplier tube through the wave-length interval  $d\lambda$ . The value of  $k$  was obtained as indicated above.

Tracings of the recordings are shown in Figure 2. Orange light ( $\lambda$  max, 630  $m\mu$ ) is seen to cut out at 11 meters, and no flashes are apparent. With the 418  $m\mu$  filter, the dark-current level of the instrument was reached at a depth of 280 meters.

The 418  $m\mu$  cast reveals an actual increase in irradiance with depth between 100 and 220 meters. Sudden flashes again occurred between 100 and 280 meters, but these, as recorded, were of lower amplitude than those in the unfiltered cast, presumably because of the narrowness and reduced intensity of the transmitted band.

These observations indicate that the light generated at depth is blue-violet (see Harvey, 1940, for spectral distribution of bioluminescence). It can be seen too (Fig. 2) that the flashes produced in the surface layers are greener.

The greater depth attained with a 418  $m\mu$  filter in the instrument (cf. Figs. 1 and 2) and the deeper flashes may be explained on the assumption that some of the light-generating constituents of the population had by then sought greater depths as the moon cleared the mountains and approached its zenith. The possibility that these constituents comprise a photoregulated community similar to the Californian deep-scattering layer may be inferred from this assumed downward migration with increasing illumination.

This inference is substantiated by observa-

tions made off San Diego (Lat. 32° 38' N., Long. 117° 35' W.) on January 17, 1956. At this time EDO fathograms and light measurements were made simultaneously during the periods of the twilight migration of the sonic-scattering layer. Figure 3A (1640–1650 hours) shows that flashes were first recorded as the photometer reached the depth of the scattering layer. Thirty minutes later (1720–1728 hours) the top of the scattering layer had reached a depth of 120 meters. Figure 3B shows that the first flashes recorded by the photometer were now at this same depth. On the day of these observations sunset was at 1706 hours.

We have recorded flashes, during our scattering-layer studies, in the Pacific, Atlantic and Mediterranean. They appear to increase both in frequency and amplitude during the twilight migration of the layer and at night. On this account it is extremely difficult to obtain an accurate picture of the spectral distribution of moonlight in the sea, or even of sunlight at scattering-layer depths.

Since the completion of this paper we have heard from Professor George L. Clarke of Harvard University (Clarke and Backus, in preparation) that he too has recorded flashes of luminescence off the Florida coast.

This phase of work on the sonic-scattering layers received additional support from the National Science Foundation and the Pauley Fund of the University of California. The inquiry was pursued from the Marine Laboratory of the University of Hawaii. The Californian data were obtained from the "USS EPCE(R) 855." Acknowledgment is made of the generous loan of the Research Vessel "Makua" by Mr. Vernon Brock, Director of the Territorial Fish and Game Commission, Hawaii. The U. S. Air Force and Marine Corps were unstinting in their loan of equipment and facilities. Data were analyzed and most of this paper was written at The Laboratory, Plymouth, England. The hospitality of the director, Mr. F. S. Russell, F. R. S., is most gratefully acknowledged. Professors



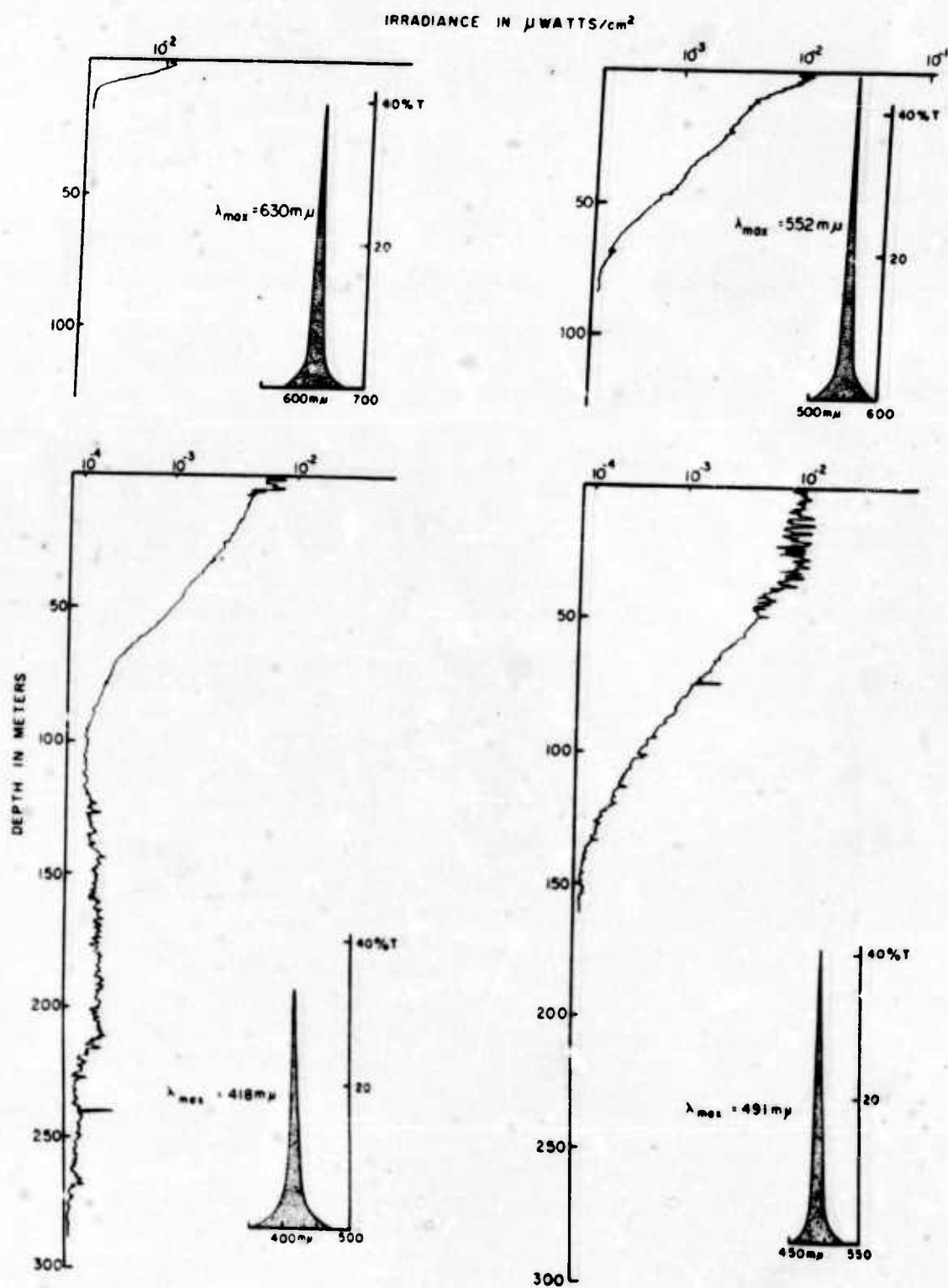


FIG. 2. Tracings of irradiance record at four different wave lengths as determined by bathyphotometer using interference filters. Inserts show measured transmission curves of filters used. The records were made at the following times:  $630\text{m}\mu$ —0020 hrs.;  $552\text{m}\mu$ —0030 hrs.;  $491\text{m}\mu$ —0044 hrs.;  $418\text{m}\mu$ —0058 hrs.; all on June 10, southwest of Oahu.

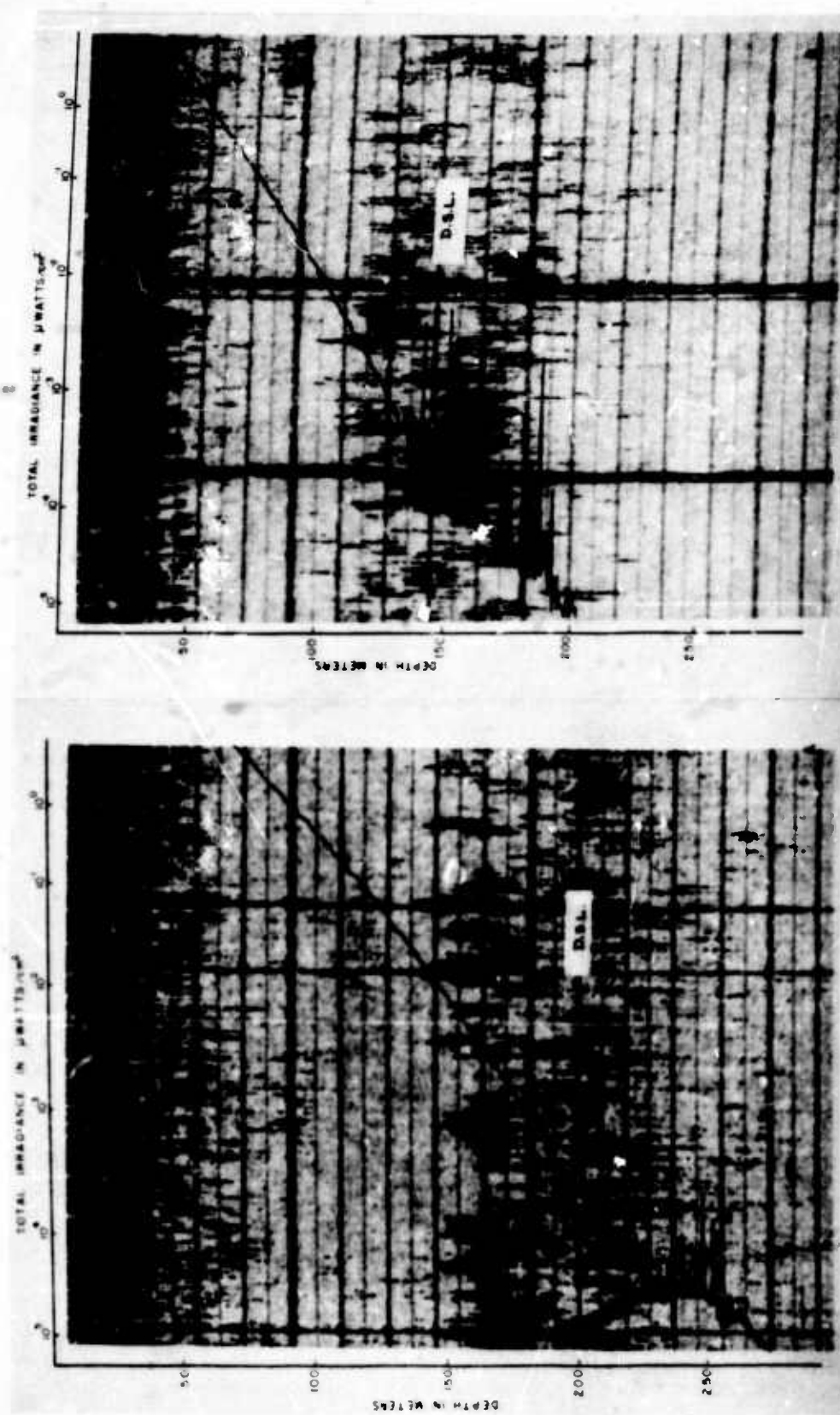


FIG. 3. Tracing of total irradiance recorded 17 January 1956, in the San Diego Trough, Latitude:  $32^{\circ} 38'$  North; Longitude:  $117^{\circ} 35'$  West. The superimposed photograms were recorded at the same time. A: 16:40-16:50 hrs. B: 17:20-17:28 hrs. The light curve does not reach the surface because the upper limit of the photometer's range is about  $24 \text{ watts}/\text{cm}^2$ .

Carl Eckart and Carl L. Hubbs of the Scripps Institution and Mr. John Tyler of the Visibility Laboratory of the Scripps Institution subjected the manuscript to vigorous and stimulating criticism.

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